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COMPREHENSIVE REVIEW

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Recent developments in *Lablab purpureus* genomics: A focus on drought stress tolerance and use of genomic resources to develop stress-resilient varieties

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Abstract

Drought is a major climatic challenge that contributes significantly to the decline of food productivity. One of the strategies to overcome this challenge is the use of drought-tolerant crops with a wide range of benefits. Lablab is a leguminous crop that has been showing high promise to drought tolerance. It is reported to have higher drought resilience compared with the commonly cultivated legumes such as common beans and cowpeas. Because of its great genetic diversity, Lablab can withstand high temperature and low rainfall, unlike other related crops. On top of that, it is grown for multitudes of purposes including food, forages, conservation agriculture, and improved soil fertility. To enhance its production and benefits during the present effects of climate change, it is crucial to develop improved varieties that would overcome the challenge of drought stress. In the past years, there have been several reviews on Lablab based on origin, domestication, characterization, utilization, germplasm conservation, some cultivation constraints, and conventional breeding with limitations on the genomic exploitation of the crop for drought tolerance. Conventional breeding is the major breeding technique for many Lablab cultivars. The integration of genomic, physiological, biochemical, and molecular approaches would be required to develop drought-tolerant cultivars of Lablab. In this review, we discuss recent developments in Lablab genomics with a focus on drought stress tolerance and the use of genomic resources to develop stress-resilient varieties.

KEYWORDS
drought tolerance, genome sequence, genomic exploitation, *Lablab purpureus*, omics technology

1 | INTRODUCTION

Global agricultural production will need to double by 2050 to meet the ever-increasing food demand especially in Africa which constitutes the fastest growing population and the second-highest growth rate in the world (AfDB, 2014; United Nations, 2019). A rise in food demand is likewise predicted due to a rise in drought stress in many parts of the world (FAO, 2017). Approximately 40% of the production land and about 50% of failures of crops have been reported due to drought stress (Fahad et al., 2017; Kapoor et al., 2020). Such an effect on agricultural production is projected in many areas especially in sub-Saharan Africa (SSA) due to

the effect of climate change (FAO, 2009; Muchuru & Nhamo, 2019; Shiferaw et al., 2014).

Maintaining production in drylands is most likely the major challenge in modern agriculture that deserves immediate intervention. Because we have some crops that perform well in drought-prone environments, the solution can involve an identification of the best cultivars and the knowledge of their drought-tolerance capability (Zandalinas et al., 2018).

Lablab (*Lablab purpureus* L. Sweet) is a drought-resilient crop with multiple benefits (Guretzki & Papenbrock, 2014; Naeem et al., 2020). It is popularly regarded as grain legume, vegetable, and fodder which is rich in protein (comparable with soybean), nutrients, and vitamins (Minde et al., 2020). In the sustainability of conserved agriculture and enhanced soil fertility, farmers have been intercropping Lablab with their major crops or utilizing it as a cover crop and green manure (Chakoma et al., 2016; Mkonda & He, 2017). The crop is a good source of rare pharmaceuticals used to cure diseases in humans and animals. It has been established recently that a carbohydrate-binding protein from Lablab can efficiently block SARS-CoV-2 and influenza viruses, thus providing room for a cure of infections (Liu et al., 2020). Insulin-like protein has also been isolated from the crop (Sachin et al., 2020). The crop also plays a great role in ensuring income security among smallholder farmers especially in dryland and semi-dryland ecosystems (Raghu et al., 2018).

The broad genetic diversity of Lablab has supported adaptation and distribution of the crop over a broad range of environmental and climatic conditions (Ewansiha et al., 2007; Venkatesha et al., 2013; Vidigal et al., 2018). It spreads along the tropical and subtropical region between 30°N and 30°S at an elevation of about 0–2000 m above sea level. Lablab also adapts to a wide range of temperature (18°C to 50°C) and annual rainfall (200–2500 mm). This is different from other related species whose favorable growth temperature ranges only between 18°C and 30°C while unable to survive in the little amount of rainfall compared with Lablab (Bhandari et al., 2017; Maass et al., 2010). Its ability to grow vigorously when rainfall resumes after drought has led to its greater resilience compared with other legumes such as common beans (*Phaseolus vulgaris*), soybeans (*Glycine max*), cowpeas (*Vigna unguiculata*), and pigeon peas (*Cajanus cajan*) (Ewansiha & Singh, 2006; Miller et al., 2018).

To enhance economic productivity and associated benefits of Lablab in the present era of frequent drought spells, there is a need of developing drought-tolerant varieties. In the past 10–15 years, detailed studies and reviews on Lablab origin, domestication, dispersal, utilization, germplasm conservation, characterization, cultivation, some production constraints, and conventional breeding have been written. The conventional breeding of many Lablab varieties was focused on improvement in soil fertility, forage, high yield, and photosensitivity while neglecting stress tolerance. The drought-tolerant traits are polygenic and possess complex nature of inheritance that would require integration of genomic, physiological, biochemical, and molecular approaches for their manipulation. Until presently, there is limited genomic information on Lablab (Rai et al., 2018b; Wang et al., 2018). In this review, we discuss recent developments in the genomics of the crop with a focus on drought stress tolerance and the use of genomic resources to develop stress-resilient varieties. This would help in improving the economic production of the crop and its associated benefits to the farming community.

2 | A BRIEF INTRODUCTION ON LABLAB GENOME

Lablab, which is also known as Dolichos Lablab (in English) and Fiwi or Ngwara (in Swahili), is a leguminous crop in the Fabaceae family. Its genome has recently been sequenced, assembled, and compared with related species (Chang et al., 2018; Iwata et al., 2013) (Table 1). The comparison shows that Lablab with chromosome numbers $2n = 2x = 20$, 22, and 24 is less complex, has a smaller genome size (367 Mb), scaffold assembly (395.47 Mb), and protein-coding genes (20,946) compared with other related species. However, these genes possess tremendous characteristics in functionality such as gene length and coding sequence which are longer compared with other species. Lablab has also longer exons and introns.

Lablab and Bambara nut were compared based on their plastid genome. While their genomes have a quadripartite structure with two inverted repeats (IRs), a large and a small single-copy region, the lengths of their plastomes are 151,753 and 152,015 bp, respectively. Each of these plastomes has four rRNAs and 71 protein-coding genes. However, their tRNA genes were not consistent in each plastome. The plastome in Lablab has 32 tRNA genes, whereas that of Bambara nut has 33 tRNA genes. Phylogenetically, Lablab was noted to relate closely with common beans (Liao et al., 2019; Wang et al., 2017). Sequenced and assembled transcriptome from Lablab was also compared with other three legumes, that is, Bambara nut, winged bean, and grass peas. The comparison revealed that the number of reads (16,190,774), transcripts (52,019), and assembled bases (51,997,858) in Lablab exceeded most of the legumes in the study. N50 of all transcripts was also higher (1570 bp) in Lablab than other legumes and thus formed a more complete assembly. This corresponded also to the highest percentage of putative orthologs in both Lablab and Bambara nut (Chapman, 2015).

3 | DROUGHT TOLERANCE IN LABLAB

3.1 | Drought-adaptive mechanisms

Crops adapt three resistance mechanisms to cope with drought, that is, drought escape, drought avoidance, and drought tolerance. For plants to escape drought conditions, they have to opt for rapid growth and development which will lead to completion of the growth cycle before drought events (Shavrukov et al., 2017). Few numbers of seeds and reduced biomass are parameters associated with *drought escape*. In *drought avoidance*, plants increase root growth while limiting their vegetative growth and transpiration rates.

TABLE 1 Genomic features (de novo sequenced genome) of Lablab and other related species

No.	Common name	Chromosome number (2n)	Genome size (Mb)	Scaffold assembled lengths (Mb)	Number of protein-coding genes	Average gene length (bp)	Average length in coding sequence (bp)	Exon length (bp)	Intron length (bp)	Reference
1	Lablab (*Lablab purpureus*)	20, 22, 24	367	395.47	20,946	3696	1276	239	557	Iwata et al. (2013); Chang et al. (2018)
2	Common bean (*Phaseolus vulgaris*)	22	587	473	27,197	-	-	-	-	Schmutz et al. (2014)
3	Cowpea (*Vigna unguiculata*)	22	613	519	29, 773	3881	-	313	-	Lonardi et al. (2019)
4	Soybean (*Glycine max*)	40	1115	950	55,137	3144	1169	232	488	Valliyodan et al. (2017); Chang et al. (2018)
5	Adzuki beans (*Vigna angularis*)	22	542	466.7	34,183	-	-	-	-	Kang et al. (2015); Yang et al. (2015)
6	Mung beans (*Vigna radiata*)	22	579	~431	22,427	-	-	-	-	Kang et al. (2014)
7	Bambara nut (*Vigna subterranean*)	22	864	535.05	31,707	3287	1163	222	501	Chang et al. (2018)
8	Pigeon pea (*Cajanus cajan*)	22	833	605.78	48,680	2348	959.35	-	-	Singh et al. (2017)
9	Groundnut (*Arachis hypogaea*)	20, 40	2552	2530	83,709	4275	226	233.21	578	Pandey et al. (2020)
10	B. trefoil (*Lotus japonicus*)	12	480	554.08	29,598	-	-	417.54	527.12	Kamal et al. (2020)
11	Acacia (*Faidherbia albida*)	26	-	653.73	28,979	3396	1207	226	504	Chang et al. (2018)
12	Marula (*Sclerocarya birrea*)	28	-	330.98	18,937	3561	1343	239	479	Bationo-kando et al. (2016); Chang et al. (2018)
13	Drumstick tree (*Moringa oleifera*)	28	-	216.76	18,451	3308	1238	232	478	Tian et al. (2015); Chang et al. (2018)
14	Barrel medic (*Medicago truncatula*)	16	390	388	50,358	2334	986	243	440	Chang et al. (2018); Young and Zhou (2020)

Note: Lablab has a smaller genome size, scaffold assembly, and protein-coding genes compared with other related species. Gene length, coding sequence, exons, and introns are longer in Lablab than in other species. This points out that Lablab has higher gene expression compared with other related species and thus suitable for genomic exploitation.

The ability of the plant to produce abundantly even under optimal water conditions is known as *drought tolerance* (Abobatta, 2019; Basu et al., 2016). Early plant vigor, fast ground cover, large seed size, long and deep root system, high root biomass, small leaflets, and high leaf water potential are some of the attributes for drought tolerance (Yadav & Sharma, 2016). This type of drought-adaptive mechanism has been noted in Lablab (Robotham & Chapman, 2015) through early or late maturing varieties. For instance, early maturing varieties can escape terminal drought, but if they are exposed to intermittent stress, they perform very poorly (Mai-Kodomi et al., 1999; Shavrukov et al., 2017). For late-maturing varieties, the sensitivity of the crop to drought stress is more during the flowering stage (Nadeem et al., 2019). These challenges can be taken care of, first by introgression of drought-tolerant attributes to the early maturing varieties, second by identifying late-maturing cultivars with drought tolerance, and third by the use of a computational model to resolve various drought scenarios influenced by climate change. Because some agro-ecological zones are not well defined in many places (Batieno, 2016),

the model should be simulated based on crop features such as growth development and yield, meteorological data, for example, temperature and rainfall and soil characteristics. Finally it can be through promoting intensified research based on the genomic potential of the selected lines.

3.2 | The basis for drought tolerance

Phenotypic plasticity in plants refers to the changes in physiological responses that contribute to their adaptability to the new environment (Alpert & Simms, 2002). The basis for such changes involves *morphological*, *biochemical*, and *molecular* mechanisms (Farooq et al., 2009). Lablab utilizes these three mechanisms to protect itself from drought stress (D'Souza & Devaraj, 2011; Guretzki & Papenbrock, 2014; Maass et al., 2010; Rangaiah & D'Souza, 2016).

Morphologically, the mechanisms include glabrous and trailing stems, a vigorous extension of shoots, shifting of leaf inclinations to reduce sun rays, decreasing in leaf sizes and structures, changing in chlorophyll contents and greenness of the crop, alterations in stomatal behavior, and their distribution to control evapotranspiration as well as deep root penetration (2 m) to the soil (Chakoma et al., 2016; USDA, 2012). There have been some "traditional (conventional)" and "improved (modern)" ways of evaluating the phenotyping effect of drought stress on Lablab (Guretzki & Papenbrock, 2013). The traditional method quantifies the effects on few accessions by analyzing their easily measurable parameters such as root parameters (e.g., length, width, and density), leaf parameters (e.g., size, number, greenish, and waxiness), plant height, stem size, and weight of fresh and dry biomass through destructive methods. The improved method can screen many accessions very efficiently without destruction. It computes the effects based on physiological processes. Some parameters that are easily computed through this method are stomatal conductivity (Grant et al., 2006), transpiration rate (Chaerle et al., 2009), and chlorophyll content (Sperdouli & Moustakas, 2012). As it demands more time and labor, the traditional method is thus regarded as less effective compared with the improved method (Golzarian et al., 2011; Honsdorf et al., 2014).

Despite many findings reported on morphological characteristics in Lablab, little has been done to correlate them with drought stress in various stages of crop development. However, there have been some drought-tolerance studies on seedlings in Lablab (D'Souza & Devaraj, 2011; Devaraj et al., 2014a, 2014b) and cowpeas (Agbicodo et al., 2009; Ajayi et al., 2017; Alidu et al., 2019; Bolarinwa et al., 2013; Muchero et al., 2008) with a limited number of accessions. Legumes are highly susceptible to drought during flowering and pod filling stages (Farooq et al., 2016; Nadeem et al., 2019). Hence, correlation studies between reproduction efficiency and drought in Lablab based on floral structure, pollination mechanisms, stigma receptivity, and grain formation are recommended.

High temperature increases reactive oxygen species (ROS) mainly hydroxyl radicals ($OH^{\cdot}$), singlet oxygen ($^1O_2$), and hydrogen peroxide (H_2O_2) that can damage physiological precursors of the crop (Foyer & Noctor, 2012; Gill & Tuteja, 2010). However, Lablab can defend against ROS biochemically via enzymatic and nonenzymatic actions (D'Souza & Devaraj, 2011). Antioxidant enzymes such as peroxidase (POX), catalase (CAT), polyphenol oxidase (PPO), glutathione reductase (GR), guaiacol peroxidase (GP), superoxide dismutase (SOD), nitric oxide, salicylic acid, and acid phosphatase (APs) play a great role in transforming ROS into less harmful chemical species (Devaraj et al., 2014a, 2014b). Non-enzymatic compounds from secondary metabolites such as flavonols, flavones, polyols, phenols, proline, glutathione (GSH), malondialdehyde (MDA), ascorbate (ASC), glycine betaines (GB), sugars, and organic solutes accumulate in the crop to regulate and protect its cellular and defense responses against drought (Rangaiah & D'Souza, 2016). Some of these enzymes have also been studied to relate them to drought tolerance in Lablab (Suzuki et al., 2012).

Molecular mechanisms of Lablab against drought stress involve upregulation and downregulation of drought-tolerant genes (Wang et al., 2018; Yao et al., 2013). This phenomenon of gene regulation has been formerly studied through molecular markers. However, the development of marker technology has been slower in Lablab and some other legumes than in cereal crops to the point of recognizing them as "orphan crops" (Dhaliwal et al., 2020; Vaijayanthi et al., 2018). In their steps of advancement, the first group of markers, amplified fragment length polymorphism (AFLP), restriction fragment length polymorphism (RFLP), and random amplification of polymorphic DNA (RAPD), was employed to understand the diversity and genetic characterization. The second group, namely, sequence-based markers including single nucleotide polymorphism (SNPs), microsatellite or simple sequence repeats (SSRs), and expressed sequence tags (ESTs), was utilized in mapping studies (Dholakia et al., 2019; Kamotho et al., 2016; Keerthi et al., 2018; Kimani et al., 2012; Konduri et al., 2000; Rai et al., 2018a; Sserumaga et al., 2021; Vaijayanthi et al., 2018). Despite their applications in Lablab, there has been little utilization of these markers to improve drought tolerance.

Based on few studies on screening for drought tolerance and utilization of markers for drought tolerance, we are evaluating seedling drought tolerance among 300 Lablab accessions at the Nelson Mandela African Institution of Science and Technology (NM-AIST), Arusha, Tanzania (Figure 1).

To offer useful knowledge in the development and transferability of markers in Lablab (Cheng et al., 2017; Jha et al., 2020; Lepcha et al., 2019), some quantitative trait loci (QTLs) for drought tolerance identified in other legumes has been presented in Table 2. This information would increase comparative knowledge, analysis, and genomic improvement of drought tolerance in Lablab.

4 | OMICS TECHNOLOGY AND RECENT GENOMIC DEVELOPMENTS

"Omics technology" is a modern molecular tool useful in recognizing functional genomic systems in an organism (Banerjee et al., 2019; Hu et al., 2018). It involves sequencing and profiling of the expressed transcripts and translated protein. Through this technology, it is easier

FIGURE 1 (a–f) Drought-tolerance evaluation of about 300 Lablab accessions at seedling stage is being carried out by the Nelson Mandela African Institution of Science and Technology (NM-AIST), Arusha, Tanzania, in a two repeating experiment. Polythene cover noted in the picture is used to induce high temperature inside the house

to expand our knowledge on various genetic processes in Lablab (Jamnadass et al., 2020; Yssel et al., 2019) and related species. Robotham and Chapman (2015) demonstrated drought-tolerance variation among Lablab germplasm through microsatellite genotyping by sequencing. Established genomic resources in Lablab by African Orphan Crops Consortium (AOCC), World Agroforestry Centre (ICRAF), Nairobi, Kenya (Chang et al., 2018), could be utilized to understand drought-tolerance mechanisms and their application in crop improvement. Some of these resources include forward and reverse Suppression Subtraction Hybridization (SSH) libraries generated from root tissues of drought-stressed Lablab accessions. This study identified 1287 unigenes from 1400 drought-induced ESTs and BhGRP1 drought-tolerant gene (Yao et al., 2013). A similar library was also developed by Wang et al. (2018) where 2792 unigenes were gathered from 4064 drought-induced ESTs. Two drought-tolerant microRNAs (miRNAs), that is, miRNA 156 and miRNA 172, were isolated from Lablab (Thilagavathy & Devaraj, 2016). As part of transcriptomic regulation for drought tolerance, the γECS gene was noted to influence the free radical system and antioxidant activities during fruit ripening in Lablab (Rai et al., 2017).

There have been also some genes, E, Dt1, GmFT2, GmGIa, PvTFLY1, and GmPhyA3, studied to relate high temperature and photoperiodic sensitivity in Lablab (Ramtekey et al., 2019). As temperature increases in many areas, flower dropping is becoming a major problem faced by farmers growing Lablab in Tanzania. It is also a common problem in other Lablab-growing areas in Africa. Although in India HA3 and HA4 Lablab varieties have been developed to overcome this challenge of flower dropping (Ramesh & Byre Gowda, 2016), genomic improvement of our cultivars based on already available resources (Ramtekey et al., 2019) would create a permanent solution (Rai et al., 2018b; Vaijayanthi et al., 2018).

5 | PROMOTING EXPLOITATION OF GENOMIC RESOURCES IN LABLAB FOR STRESS TOLERANCE

Lablab is increasingly becoming a popular crop in the community due to its multitude of values. The crop has therefore been engaged in several research programs, many of them taking place in Asia rather than Africa where the crop originates (Maass, 2016; Maass et al., 2010). Among research happening in Africa, it is only little or none that has been directed to the genomic development affecting the release of varieties for commercial purposes. So far, many of the world-known commercial varieties in Lablab, for example, Koala, HA3, and HA4 for grains and Rongai, Endurance, and Highworth for forage, come from Asia and Australia (Gopalakrishnan, 2007; Maass et al., 2010; Ramesh & Byre Gowda, 2016). In Africa, only Kenya has commercialized its varieties: Eldo-KT Black 1 and 2 (Eldoret Kirkhouse Trust black), Eldo-KT cream, and Eldo-KT Maridadi (KEPHIS, 2017; Kirkhouse Trust, 2015). Evaluation performance of the promising cultivars has also been taking place in Northern Tanzania towards their commercialization (Miller et al., 2018; Nord et al., 2020). The reason behind these few recommended varieties was research focusing more on morphological characterization, forage, and soil properties especially in Africa.

Making genomic information of Lablab easily available such as the AOCC (Hendre et al., 2019) will provide inputs for translational

TABLE 2 Molecular markers and QTLs for drought tolerance in some other legumes

No.	Crop	Molecular markers/QTLs	Mapping population	Features in drought tolerance	Reference
1	Common beans	SSR; AFLP markers; 49 QTLs	82 recombinant inbred lines (RILs)	Drought-responsive agronomic traits	Sedlar et al. (2020)
		SNP markers; 18 QTLs	97 RIL from parent lines: Portillo × red hawk	Drought-tolerance parameters	Onziga et al. (2019)
		SSR and SNP markers; 12 QTLs	F8; SEA 5 × AND 277	Drought (stress) conditions	Briñez et al. (2017)
		SSR; 69 QTLs SSR; 15 putative QTLs	DOR364 × BAT477	Drought-tolerance parameters; root-drought-related traits	Asfaw and Blair (2012)
		AFLP, RAPD, SSR markers; 143 QTLs	100 RILs	Drought-tolerance and drought-related traits	Diaz et al. (2018)
		SNP markers; 14 QTLs	RILs; SEA5 × CAL96	Phenology-yield-drought	Mukeshimana et al. (2014)
		53 SNP markers; 11 QTLs	128-F8 RILs	Drought stress conditions	Nabateregga et al. (2019)
		SNP markers; genes functioning	Pinto-Villa × Pinto Saltillo, F3:5 (289 genotypes)	Drought tolerance	Villordo-Pineda et al. (2015)
2	Cowpeas	184 genome-wide EST-derived SNP markers; drought-tolerance QTLs	2 drought-tolerant lines (IT93K-503-1 and IT97K-499-35)	Green abilities and yield under water stress conditions	Batieno et al. (2016)
		412 DArT, 80 AFLP, 28 microsatellite markers; 2 QTLs	72-F1 derived double haploid (DH)	Stress tolerance (drought)	Fan et al. (2015)
		35 SNP markers; tolerance index ranged between 69.19 and 142.01	305-F8 RILs	Tolerance to water-deficit conditions	Ravelombola et al. (2021)
3	Chickpeas	SNP markers and 21 major QTLs	232 RILs; ICC 4958 × ICC 1882	Drought-tolerance parameters	Sivasakthi et al. (2018)
		828 SNPs; DREB and CAPS from QTL-hotspot region	264 RILs	Drought tolerance	Jaganathan et al. (2015)
		47, 53, and 46 SSR markers in selection; QTL-hotspot region	3 elite cultivars	Drought tolerance and grain yield	Bharadwaj et al. (2021)
4	Soybeans	368 SSR including Satt277; QTLs	F2 mapping population (PK1180, SL 46 × UPSL 298, PK 1169)	Seedling survivability under drought conditions	Sreenivasa et al. (2020)
		8078 specific locus amplified fragments (SLAF) markers; 23 QTLs	RILs	Drought-tolerance traits	Ren et al. (2020)
5	Mung bean	3690 SSR; 58 QTLs for plant parameters and 5 for drought tolerance	256 RIL population	Plant tolerance and associated parameters	Liu et al. (2017)
6	Asparagus bean	39 SNPs markers from GWAS	95 accessions	Tolerance to soil water stress	Xu et al. (2015)

Note: Some QTLs and molecular markers from some commonly grown legumes that could provide useful knowledge in their transferability in Lablab.
Abbreviations: AFLP, amplified fragment length polymorphism; QTLs, quantitative trait loci; RAPD, random amplification of polymorphic DNA; SNP, single nucleotide polymorphism; SSR, simple sequence repeat.

research on its sustainable development. However, we need further bioinformatics training among researchers for the efficient use of genomic databases. Moreover, the adoption of high-throughput technologies such as next-generation, genome-wide association studies (GWAS), transcript profiling, and gene and genomic editing (CRISPR/cas9) will bring discovery of more drought-tolerant genes and their expressed quantitative loci (eQTLs). Increased deployment of these genomic tools with an increase of research collaboration will also bring a new revolution in farming systems of drylands (Njarui & Mureithi, 2010; Sennhenn et al., 2017). One of the benefits of using new drought-tolerant varieties is to protect their productivity in dry environments against increased aridity and semiaridity conditions especially in SSA where desertification is highly concerned. As already predicted that desertification will increase as noted in the Saharan

desert that keeps spreading to the south, sensitization of Lablab production to the region would be an important opportunity to minimize the effects of drought stress on the region. In return, production will get improved to make it more commercialized.

Genomic exploitations of Lablab cannot become successful if there is a limitation of genetic resources. This is because, useful resources for exploitation come from a wide range of genetic materials (Azeez et al., 2018). Collections of genetic resources have been the role of the National Plant Genetic Resource Centers (NPGRCs) and local and international research institutions. Whereas the largest world collections of Lablab accessions (650) have been held at the University of Agricultural Sciences (UAS), Bengaluru, India (Ramesh & Byre Gowda, 2016), the NM-AIST, Arusha, Tanzania, has the largest collections (450) of Lablab in Africa (Kirkhouse Trust, 2019). This shows that Africa has fewer collections of resources compared with Asia.

These resources could be enhanced through an exchange of exotic materials and collections of local farmers' landraces. Because they are the populations of historical origin with distinct identities, farmers' landraces have been preferred in genomic exploitation for drought tolerance as they are more adapted to abiotic challenges and well connected to farming practices. Despite their roles in stress resilience, their collections have not been sufficiently exhausted in many countries. Several NPGRCs still lack them to a high extent. Little collections available at the centers are neither comprehensive nor representative of the genetic diversity available from their local context. This is because their collection missions are donor driven with many of them influenced by external needs. Even when collections are done by local personnel for research purposes, there has been a tendency to introduce them from international gene banks. These local resources have also been lost in developing countries due to urbanization and abandonment of farming activities for the farmers' interest of moving to towns and cities for small jobs and business. To handle this challenge, we need a strong collaboration among all stakeholders; farmers, researchers, government, and international agencies that will efficiently control in situ and ex situ conservation of the resources.

6 | CONCLUSION

Lablab is exhibiting an increased research interest due to its wide range of benefits. It has shown a great ability to withstand drought stress compared with other related species. Despite this advantage, there has been very little effort in exploitation of genomic resources in Lablab for drought tolerance. As a result, the crop has been underutilized in many areas. However, because of this genomic potential, the development of the crop through an application of "omics" technology is proposed so that we can convert it into a commercialized crop. The challenge behind this mission is the high cost for most of the tools in "omics technology." Additionally, the methods are time consuming, requiring very expensive consumables, and not feasible for a quick response. Reducing their running cost while deploying cheap and simple tools such as Nanopore MinION field sequencer would lead to the best findings. With sustainable utilization of genomic resources in Lablab, the crop can be transformed from an orphan legume into an industrial crop.

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CONFLICT OF INTEREST

None.

ETHICS STATEMENT

This manuscript does not contain any studies with human or animal subjects.

DATA AVAILABILITY STATEMENT

No new data were created or analyzed in this study.

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REFERENCES

Abobatta, W. F. (2019). Drought adaptive mechanisms of plants—A review. *Advances in Agriculture and Environmental Science*, *2*(1), 62–65. https://doi.org/10.30881/aaeoa.00022

AfDB. (2014). Tracking Africa's growth in figures. Statistics Department, African Development Bank, Tunis, Tunisia.

Agbicodo, E. M., Fatokun, C. A., Muranaka, S., Visser, R. G. F., & van der Linden, C. G. (2009). Breeding drought tolerant cowpea: Constraints, accomplishments, and future prospects. *Euphytica*, *167*(3), 353–370. https://doi.org/10.1007/s10681-009-9893-8

Ajayi, A. T., Olumekun, V. O., & Gbabamosi, A. E. (2017). Estimates of genetic variation among drought tolerant traits of cowpea at seedling stage. *International Journal of Plant Research*, *7*(2), 48–57. https://doi.org/10.5923/j.plant.20170702.04

Alidu, M. S., Asante, I. K., Tongoona, P., Ofori, K., Danquah, A., & Padi, F. K. (2019). Development and screening of cowpea recombinant inbred lines for seedling drought tolerance. *Journal of Plant Breeding and Crop Science*, *11*(1), 1–10. https://doi.org/10.5897/JPBCS2018.0768

Alpert, P., & Simms, E. L. (2002). The relative advantages of plasticity and fixity in different environments: When is it good for a plant to adjust? *Evolutionary Ecology*, *16*(3), 285–297. https://doi.org/10.1023/A:1019684612767

Asfaw, A., & Blair, M. W. (2012). Quantitative trait loci for rooting pat-tern traits of common beans grown under drought stress versus non-stress conditions. *Molecular Breeding*, *30*(2), 681–695. https://doi.org/10.1007/s11032-011-9654-y

Azeez, M. A., Adubi, A. O., & Durodola, F. A. (2018). Landraces and crop genetic improvement. In *Rediscovery of Landraces as a Resource for the Future*. London, UK: Oscar Grillo, IntechOpen. https://www.intechopen.com/books/rediscovery-of-landraces-as-a-resource-for-the-future/landraces-and-crop-genetic-improvement

Banerjee, R., Kumar, G. V., & Kumar, S. P. J. (2019). *OMICS-based approaches in plant biotechnology*. Scrivener Publishing. https://doi.org/10.1002/9781119509967

Basu, S., Ramegowda, V., Kumar, A., & Pereira, A. (2016). Plant adaptation to drought stress [version 1; referees: 3 approved]. *F1000Research*, *5*(1554), 1–10. https://doi.org/10.12688/f1000research.7678.1

Batieno, B. J., Danquah, E., Tignegre, J., Huynh, B., Drabo, I., Close, T. J., … Ouedraogo, T. J. (2016). Application of marker-assisted backcrossing to improve cowpea (*Vigna unguiculata* L. Walp) for drought tolerance. *Journal of Plant Breeding and Crop Science*, *8*(12), 273–286. https://doi.org/10.5897/JPBCS2016.0607

Batieno, J. (2016). Evolution of Burkina agro-ecological zone. In J. Ouedraogo, P. Ndakidemi, & P. Venkataramana (Eds.), *Stress Tolerant Orphan Legumes. PanAfrican Grain Legume and World Cowpea Conference* (pp. 14–16). London, UK: Kirkhouse Trust. http://gl2016conf.iita.org/wp-content/uploads/2016/03/PLENARY-Stress-Tolerant-Orphan-Legumes-J-Ouedraogo-et-al.pdf

Bationo-kando, P., Zongo, J., & Siljak-yakovlev, S. (2016). First genome size assessment, heterochromatin and rDNA chromosome mapping in the genus *Sclerocarya* (Anacardiaceae): Insight into the new basic chromosome number. *Botany Letters*, *163*(1), 1–7. https://doi.org/10.1080/12538078.2015.1132008

Bhandari, K., Sharma, K. D., Rao, B. H., Siddique, K. H. M., Gaur, P., Agrawal, S. K., … Nayyar, H. (2017). Temperature sensitivity of food legumes: A physiological insight. *Acta Physiologiae Plantarum*, *39*, 2–22. https://doi.org/10.1007/s11738-017-2361-5

Bharadwaj, C., Tripathi, S., Soren, K. R., Thudi, M., Singh, R. K., Sheoran, S., … Varshney, R. K. (2021). Introgression of "QTL-hotspot" region enhances drought tolerance and grain yield in three elite chickpea cultivars. *Plant Genome*, *14*, e20076. https://doi.org/10.1002/tpg2.20076

Bolarinwa, K. A., Ogunkanmi, L. A., Adetumbi, J. A., Akinyosoye, S. T., Akande, S. R., & Amusa, O. D. (2013). Screening of cowpea lines for drought tolerance. Proceedings of the 37th Annual Conference of Genetics Society of Nigeria (GSN), Lafia, (21st–24th October), *PGB14*: 29–37 (Nigeria).

Briñez, B., Perseguini, J. M. K. C., Rosa, J. S., Bassi, D., Gonçalves, J. G. R., Almeida, C., … Benchimol-Reis, L. L. (2017). Mapping QTLs for drought tolerance in a SEA 5 x AND 277 common bean cross with SSRs and SNP markers. *Genetics and Molecular Biology*, *40*(4), 813–823. https://doi.org/10.1590/1678-4685-GMB-2016-0222

Chaerle, L., Lenk, S., Leinonen, I., Jones, H. G., van Der Straeten, D., & Buschmann, C. (2009). Multi-sensor plant imaging: Towards the development of a stress-catalogue. *Biotechnology Journal*, *4*(8), 1152–1167. https://doi.org/10.1002/biot.200800242

Chakoma, I., Manyawu, G., Gwiriri, L., Moyo, S., & Sikhalazo, D. (2016). The agronomy and use of *Lablab purpureus* in smallholder farming systems of southern Africa. ILRI Extension Brief, (December), 1–4.

Chang, Y., Liu, H., Liu, M., Liao, X., Sahu, S. K., Fu, Y., … Liu, X. (2018). The draft genomes of five agriculturally important African orphan crops. *GigaScience*, *8*, 1–16. https://doi.org/10.1093/gigascience/giy152

Chapman, M. A. (2015). Transcriptome sequencing and marker development for four underutilized legumes. *Applications in Plant Sciences*, *3*(2), 1400111. https://doi.org/10.3732/apps.1400111

Cheng, A., Chai, H. H., Ho, W. K., Bamba, A. S. A., Feldman, A., Kendabie, P., … Massawe, F. (2017). Molecular marker technology for genetic improvement of underutilised crops. In S. Abdullah, H. Chai-Ling, & C. Wagstaff (Eds.), *Crop improvement* (pp. 47–70). Springer. https://doi.org/10.1007/978-3-319-65079-1_3

Devaraj, V. R., D'souza, M. R., & Kokila, S. (2014a). Polyamine levels in leaves of hyacinth bean (*Lablab purpureus*) and their relation to drought-tolerance. *World Applied Sciences Journal*, *32*(58), 2398–2402. https://doi.org/10.5829/idosi.wasj.2014.32.12.1382

Devaraj, V. R., D'souza, M. R., & Kokila, S. (2014b). Response of *Lablab purpureus* (hyacinth bean) cultivars to drought stress. *Pelagia Research Library Asian Journal of Plant Science and Research*, *4*(5), 48–55.

Dhaliwal, S. K., Talukdar, A., Gautam, A., Sharma, P., Sharma, V., & Kaushik, P. (2020). Developments and prospects in imperative under-exploited vegetable legumes breeding: A review. *International Journal of Molecular Sciences*, *21*, 9615. https://doi.org/10.3390/ijms21249615

Dholakia, H. P., Joshi, M. K., & Delvadiya, I. R. (2019). Molecular characterization of Indian bean (*Lablab purpureus* L.) genotypes. *Journal of Pharmacognosy and Phytochemistry*, *8*(2), 455–463.

Diaz, L. M., Ricaurte, J., Tovar, E., Cajiao, C., Teran, H., Grajales, M., Polanía, J., Rao, I., Beebe, S., & Raatz, B. (2018). QTL analyses for tolerance to abiotic stresses in a common bean (*Phaseolus vulgaris* L.) population. *PLoS ONE*, *13*(8), e0202342. https://doi.org/10.1371/journal.pone.0202342

D'Souza, M. R., & Devaraj, V. R. (2011). Specific and non-specific responses of hyacinth bean (*Dolichos lablab*) to drought stress. *Indian Journal of Biotechnology*, *10*(1), 130–139.

Ewansiha, S. U., Chiezey, U. F., Tarawali, S. A., & Iwuafor, E. N. O. (2007). Morpho-phenological variation in *Lablab purpureus*. *Tropical Grasslands*, *41*(4), 277–284.

Ewansiha, S. U., & Singh, B. B. (2006). Relative drought tolerance of important herbaceous legumes and cereals in the moist and semi-arid regions of West Africa. *Journal of Food, Agriculture and Environment*, *4*(2), 188–190.

Fahad, S., Bajwa, A. A., Nazir, U., Anjum, S. A., Farooq, A., Zohaib, A., … Huang, J. (2017). Crop production under drought and heat stress: Plant responses and management options. *Frontiers in Plant Science*, *8*(June), 1–16. https://doi.org/10.3389/fpls.2017.01147

Fan, Y., Shabala, S., Ma, Y., Xu, R., & Zhou, M. (2015). Using QTL mapping to investigate the relationships between abiotic stress tolerance (drought and salinity) and agronomic and physiological traits. *BMC Genomics*, *16*, 43. https://doi.org/10.1186/s12864-015-1243-8

FAO. (2009). Climate change in Africa: The threat to agriculture. Accra: FAO Regional Office for Africa. Accra, Ghana. 1-7pp. https://www.uncclearn.org/wp-content/uploads/library/fao34.pdf

FAO. (2017). In Food and Agriculture Organization (FAO) of the United Nations. (Ed.), *The future of food and agriculture: Trends and challenges*. Rome, Italy: FAO. http://www.fao.org/3/i6583e/i6583e.pdf

Farooq, M., Gogoi, N., Barthakur, S., Baroowa, B., Bharadwaj, N., Alghamdi, S. S., & Siddique, K. H. M. (2016). Drought stress in grain legumes during reproduction and grain filling. *Journal of Agronomy and Crop Science*, *203*(2), 81–102. https://doi.org/10.1111/jac.12169

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., & Basra, S. M. A. (2009). Plant drought stress: Effects, mechanisms and management. *Agronomy for Sustainable Development*, *29*(1), 185–212. https://doi.org/10.1051/agro:2008021

Foyer, C. H., & Noctor, G. (2012). Managing the cellular redox hub in photosynthetic organisms. *Plant, Cell and Environment*, *35*(2), 199–201. https://doi.org/10.1111/j.1365-3040.2011.02453.x

Gill, S. S., & Tuteja, N. (2010). Reactive oxygen species and antioxidant machinery in abiotic stress tolerance in crop plants. *Plant Physiology and Biochemistry*, *48*(12), 909–930. https://doi.org/10.1016/j.plaphy.2010.08.016

Golzarian, M. R., Frick, R. A., Rajendran, K., Berger, B., Roy, S., Tester, M., & Lun, D. S. (2011). Accurate inference of shoot biomass from high-throughput images of cereal plants. *Plant Methods*, *7*(1), 1–11. https://doi.org/10.1186/1746-4811-7-2

Gopalakrishnan, T. R. (2007). Vegetable crops. In *Legume vegetables*. Horticulture Science Series 4. (pp. 169–198). New India Publishing Agency.

Grant, O. M., Chaves, M. M., & Jones, H. G. (2006). Optimizing thermal imaging as a technique for detecting stomatal closure induced by drought stress under greenhouse conditions. *Physiologia Plantarum*, *127*(3), 507–518. https://doi.org/10.1111/j.1399-3054.2006.00686.x

Guretzki, S., & Papenbrock, J. (2013). Comparative analysis of methods analyzing effects of drought on the herbaceous plant *Lablab purpureas*. *Journal of Applied Botany and Food Quality*, *86*(1), 47–54. https://doi.org/10.5073/JABFQ.2013.086.007

Guretzki, S., & Papenbrock, J. (2014). Characterization of *Lablab purpureus* regarding drought tolerance, trypsin inhibitor activity and cyanogenic potential for selection in breeding programmes. *Journal of Agronomy and Crop Science*, *200*(1), 24–35. https://doi.org/10.1111/jac.12043

Hendre, P. S., Muthemba, S., Kariba, R., Muchugi, A., Fu, Y., Chang, Y., … Jamnadass, R. (2019). African Orphan Crops Consortium (AOCC): Status of developing genomic resources for African orphan crops. *Planta*, *250*, 989–1003. https://doi.org/10.1007/s00425-019-03156-9

Honsdorf, N., March, T. J., Berger, B., Tester, M., & Pillen, K. (2014). High-throughput phenotyping to detect drought tolerance QTL in wild barley introgression lines. *PLoS ONE*, *9*(5), e97047. https://doi.org/10.1371/journal.pone.0097047

Hu, H., Scheben, A., & Edwards, D. (2018). Advances in integrating genomics and bioinformatics in the plant breeding pipeline. *Agriculture-Basel*, *8*, 75.

Iwata, A., Greenland, C. M., & Jackson, S. A. (2013). Cytogenetics of legumes in the Phaseoloid clade. *Plant Genome*, *6*(3), 3. https://doi.org/10.3835/plantgenome2013.03.0004

Jaganathan, D., Thudi, M., Kale, S., Azam, S., Roorkiwal, M., Gaur, P. M., … Varshney, R. K. (2015). Genotyping-by-sequencing based intra-specific genetic map refines a "QTL-hotspot" region for drought tolerance in chickpea. *Molecular Genetics and Genomics*, *290*(2), 559–571. https://doi.org/10.1007/s00438-014-0932-3

Jamnadass, R., Mumm, R. H., Hale, I., Hendre, P., Muchugi, A., Dawson, I. K., … Van Deynze, A. (2020). Enhancing African orphan crops with genomics. *Nature Genetics*, *52*(4), 356–360. https://doi.org/10.1038/s41588-020-0601-x

Jha, U. C., Bohra, A., & Nayyar, H. (2020). Advances in "omics" approaches to tackle drought stress in grain legumes. *Plant Breeding*, *139*, 1–27. https://doi.org/10.1111/pbr.12761

Kamal, N., Mun, T., Reid, D., Lin, J. S., Akyol, T. Y., Sandal, N., … Andersen, S. U. (2020). Insights into the evolution of symbiosis gene copy number and distribution from a chromosome-scale *Lotus japonicus* Gifu genome sequence. *DNA Research*, *27*(3), dsaa015. https://doi.org/10.1093/dnares/dsaa015

Kamotho, G. N., Kinyua, M. G., Muasya, R. M., Gichuki, S. T., & Wanjala, B. W. (2016). Assessment of genetic diversity of Kenyan Dolichos bean (*Lablab purpureus* L. Sweet) using simple sequence repeat (SSR) markers. *International Journal of Agriculture, Environment and Bioresearch*, *1*(01), 26–43.

Kang, Y. J., Kim, S. K., Kim, M. Y., Lestari, P., Kim, K. H., Ha, B. K., … Lee, S. H. (2014). Genome sequence of mungbean and insights into evolution within Vigna species. *Nature Communications*, *5*, 5443. https://doi.org/10.1038/ncomms6443

Kang, Y. J., Satyawan, D., Shim, S., Lee, T., Lee, J., Hwang, W. J., … Lee, S. H. (2015). Draft genome sequence of adzuki bean, *Vigna angularis*. *Scientific Reports*, *5*, 8069. https://doi.org/10.1038/srep08069

Kapoor, D., Bhardwaj, S., Landi, M., Sharma, A., Ramakrishnan, M., & Sharma, A. (2020). The impact of drought in plant metabolism: How to exploit tolerance mechanisms to increase crop production. *Applied Sciences*, *10*(5692), 1–19. https://doi.org/10.3390/app10165692

Keerthi, C. M., Ramesh, S., Byregowda, M., & Vaijayanthi, P. V. (2018). Simple sequence repeat (SSR) marker assay-based genetic diversity among Dolichos bean (*Lablab purpureus* L. sweet) advanced breeding lines differing for productivity per se traits. *International Journal of Current Microbiology and Applied Sciences*, *7*(5), 3736–3744. https://doi.org/10.20546/ijcmas.2018.705.433

KEPHIS. (2017). National crop variety list-Kenya. Retrieved August 19, 2019, from Kenya Plant Health Inspectorate Service, Nairobi website: http://www.kephis.org/images/VarietyList/april20170525.pdf

Kimani, E. N., Wachira, F. N., & Kinyua, M. G. (2012). Molecular diversity of Kenyan lablab bean (*Lablab purpureus* (L.) Sweet) accessions using amplified fragment length polymorphism markers. *American Journal of Plant Sciences*, *3*, 313–321. https://doi.org/10.4236/ajps.2012.33037

Kirkhouse Trust. (2015). Dolichos improvement programme in Kenya. *Kirkhouse Times*, 1–6.

Kirkhouse Trust. (2019). Supporting research and education in biological sciences: Agricultural crop improvement for the relief of poverty, with a focus on legumes. Retrieved September 10, 2019, from Stress Tolerant Orphan Legumes. PanAfrican Grain Legume and World Cowpea Conference; Livingstone, Zambia; March, 2016 Legumes (STOL) Project at NM-IAST, Arusha, Tanzania. Website: https://www.kirkhousetrust.org/stolprojects

Konduri, V., Godwin, I. D., & Liu, C. J. (2000). Genetic mapping of the *Lablab purpureus* genome suggests the presence of 'cuckoo' gene(s) in this species. *Theoretical and Applied Genetics*, *100*, 866–871. https://doi.org/10.1007/s001220051363

Lepcha, P., Kumar, P. R., & Sathyanarayana, N. (2019). Exploring genomics research in the context of some underutilized legumes - A review. In R. Banerjee, G. V. Kumar, & S. P. J. Kumar (Eds.), *OMICS - Based approaches in plant biotechnology* (Vol. 333, 1st ed., pp. 1–18). Wiley-Scrivener. https://doi.org/10.1002/9781119509967.ch1

Liao, X., Liu, Y., & Liu, H. (2019). The complete plastid genomes of two Fabaceae orphan crops from Africa. *Mitochondrial DNA Part B*, *4*(1), 93–94. https://doi.org/10.1080/23802359.2018.1536481

Liu, C., Wu, J., Wang, L., Fan, B., Cao, Z., Su, Q., … Wang, S. (2017). Quantitative trait locus mapping under irrigated and drought treatments based on a novel genetic linkage map in mungbean (*Vigna radiata* L.). *Theoretical and Applied Genetics*, *130*, 2375–2393. https://doi.org/10.1007/s00122-017-2965-6

Liu, Y. M., Shahed-Al-Mahmud, M., Chen, X., Chen, T. H., Liao, K. S., Lo, J. M., … Ma, C. (2020). A carbohydrate-binding protein from the edible lablab beans effectively blocks the infections of influenza viruses and SARS-CoV-2. *Cell Reports*, *32*, 108016. https://doi.org/10.1016/j.celrep.2020.108016

Lonardi, S., Muñoz-Amatriaín, M., Liang, Q., Shu, S., Wanamaker, S. I., Lo, S., … Close, T. J. (2019). The genome of cowpea (*Vigna unguiculata* [L.] Walp.). *The Plant Journal*, *98*(5), 767–782. https://doi.org/10.1111/tpj.14349

Maass, B. L. (2016). Origin, domestication and global dispersal of *Lablab purpureus* (L.) Sweet (Fabaceae): Current understanding. *Legume Perspectives*, *13*, 5–8.

Maass, B. L., Knox, M. R., Venkatesha, S. C., Angessa, T. T., Ramme, S., & Pengelly, B. C. (2010). *Lablab purpureus*—A crop lost for Africa? *Tropical Plant Biology*, *3*(3), 123–135. https://doi.org/10.1007/s12042-010-9046-1

Mai-Kodomi, Y., Singh, B. B., Myers, O., Yopp, J. H., Gibson, P. J., & Terao, T. (1999). Two mechanisms of drought tolerance in cowpea. *Indian Journal of Genetics*, *59*, 309–316.

Miller, N. R., Mariki, W., Nord, A., & Snapp, S. (2018). Cultivar selection and management strategies for *Lablab purpureus* (L.) Sweet in Africa. In *Handbook of Climate Change Resilience*. Springer, Cham. https://doi.org/10.1007/978-3-319-71025-9_102-1

Minde, J. J., Venkataramana, P. B., Matemu, A. O., Minde, J. J., Venkataramana, P. B., & Matemu, A. O. (2020). *Dolichos lablab*—An underutilized crop with future potentials for food and nutrition security: A review. *Critical Reviews in Food Science and Nutrition*, 1–13. https://doi.org/10.1080/10408398.2020.1775173

Mkonda, M., & He, X. (2017). Conservation agriculture in Tanzania. *Sustainable Agriculture Reviews*, *22*, 310–324. https://doi.org/10.1007/978-3-319-48006-0

Muchero, W., Ehlers, J. D., & Roberts, P. A. (2008). Seedling stage drought-induced phenotypes and drought-responsive genes in diverse cowpea genotypes. *Crop Science*, *48*(2), 541–552. https://doi.org/10.2135/cropsci2007.07.0397

Muchuru, S., & Nhamo, G. (2019). A review of climate change adaptation measures in the African crop sector. *Climate and Development*, *11*(10), 873–885. https://doi.org/10.1080/17565529.2019.1585319

Mukeshimana, G., Butare, L., Cregan, P. B., Blair, M. W., & Kelly, J. D. (2014). Quantitative trait loci associated with drought tolerance in common bean (*Phaseolus vulgaris*). *Crop Science*, *54*(3), 923–938. https://doi.org/10.2135/cropsci2013.06.0427

Nabateregga, M., Mukankusi, C., Raatz, B., Edema, R., Nkalubo, S., & Alladassi, B. M. E. (2019). Quantitative trait loci (QTL) mapping for intermittent drought tolerance in BRB 191 × SEQ 1027 Andean Intragene cross recombinant inbred line population of common bean (*Phaseolus vulgaris* L.). *African Journal of Biotechnology*, *18*(21), 452–461. https://doi.org/10.5897/AJB2019.16768

Nadeem, M., Li, J., Yahya, M., Sher, A., Ma, C., Wang, X., & Qiu, L. (2019). Research progress and perspective on drought stress in legumes: A review. *International Journal of Molecular Sciences*, *20*(10), 1–32. https://doi.org/10.3390/ijms20102541

Naeem, M., Shabbir, A., Ansari, A. A., Aftab, T., Khan, M. M., & Uddin, M. (2020). Scientia Horticulturae hyacinth bean (Lablab purpureus L.) – An underutilised crop with future potential. *Scientia Horticulturae*, *272*, 109551. https://doi.org/10.1016/j.scienta.2020.109551

Njarui, D. M. G., & Mureithi, J. G. (2010). Evaluation of lablab and velvet bean fallows in a maize production system for improved livestock feed supply in semiarid tropical Kenya. *Animal Production Science*, *50*(3), 193–202. https://doi.org/10.1071/AN09137

Nord, A., Miller, N. R., Mariki, W., Drinkwater, L., & Snapp, S. (2020). Investigating the diverse potential of a multi-purpose legume, Lablab purpureus (L.) Sweet, for smallholder production in East Africa. *PLoS ONE*, *15*(1), e0227739. https://doi.org/10.1371/journal.pone.0227739

Onziga, I. D., Nkalubo, S. T., & Kelly, J. D. (2019). Identification of QTL associated with drought tolerance in Andean common bean. *Crop Science*, *59*, 1–14. https://doi.org/10.2135/cropsci2018.10.0604

Pandey, M. K., Pandey, A. K., Kumar, R., Nwosu, C. V., Guo, B., Wright, G. C., … Zhuang, W. (2020). Translational genomics for achieving higher genetic gains in groundnut. *Theoretical and Applied Genetics*, *133*(5), 1679–1702. https://doi.org/10.1007/s00122-020-03592-2

Raghu, B. R., Samuel, D. K., Mohan, N., & Aghora, T. S. (2018). Dolichos bean: An underutilized and unexplored crop with immense potential. *International Journal of Recent Advances in Multidisciplinary Research*, *05*(12), 4338–4341.

Rai, K. K., Rai, N., & Rai, S. P. (2017). Downregulation of *γECS* gene affects antioxidant activity and free radical scavenging system during pod development and maturation in *Lablab perpureus* L. *Biocatalysis and Agricultural Biotechnology*, *2017*(March), 192–200. https://doi.org/10.1016/j.bcab.2017.07.005

Rai, K. K., Rai, N., & Rai, S. P. (2018a). Investigating the impact of high temperature on growth and yield of *Lablab purpureus* L. inbred lines using integrated phenotypical, physiological, biochemical and molecular approaches. *Indian Journal of Plant Physiology*, *23*, 209–226. https://doi.org/10.1007/s40502-018-0364-x

Rai, K. K., Rai, N., & Rai, S. P. (2018b). Recent advancement in modern genomic tools for adaptation of *Lablab purpureus* L to biotic and abiotic stresses: Present mechanisms and future adaptations. *Acta Physiologiae Plantarum*, *40*(9), 164. https://doi.org/10.1007/s11738-018-2740-6

Ramesh, S., & Byre Gowda, M. (2016). Dolichos bean (*Lablab purpureus* L. Sweet, var. Lignosus) genetics and breeding—Present status and future prospects. *Mysore Journal of Agricultural Sciences*, *50*, 481–500.

Ramtekey, V., Bhuriya, A., Ayer, D., Parekh, V., Modha, K., & Kale, B. (2019). Molecular tagging of photoperiod responsive flowering in Indian bean [*Lablab purpureus* (L.) Sweet]. *Journal of Genetics*, *79*(1), 264–269. https://doi.org/10.31742/IJGPB.79S.1.17

Rangaiah, D. V., & D'Souza, M. (2016). Hyacinth bean (*Lablab purpureus*): An adept adaptor to adverse environments. *The Journal of the International Legume Society*, *13*, 20–22.

Ravelombola, W., Shi, A., & Huynh, B. (2021). Loci discovery, network-guided approach, and genomic prediction for drought tolerance index in a multi-parent advanced generation intercross (MAGIC) cowpea population. *Horticulture Research*, *8*, 24. https://doi.org/10.1038/s41438-021-00462-w

Ren, H., Han, J., Wang, X., Zhang, B., Yu, L., Gao, H., … Qiu, L. J. (2020). QTL mapping of drought tolerance traits in soybean with SLAF sequencing. *The Crop Journal.*, *8*, 977–989. https://doi.org/10.1016/j.cj.2020.04.004

Robotham, O., & Chapman, M. (2015). Population genetic analysis of hyacinth bean (*Lablab purpureus* (L.) Sweet, Leguminosae) indicates an East African origin and variation in drought tolerance. *Genetic Resources and Crop Evolution*, *64*(1), 139–148. https://doi.org/10.1007/s10722-015-0339-y

Sachin, P., Behnaz, P., Anjali, A., & Anushree, L. (2020). PCR based detection of insulin like protein from *Dolichos lablab* L. *Journal of Stress Physiology & Biochemistry*, *16*(2), 81–85.

Schmutz, J., Mcclean, P. E., Mamidi, S., Wu, G. A., Cannon, S. B., Grimwood, J., Jenkins, J., Shu, S., Song, Q., Chavarro, C., Torres-Torres, M., Geffroy, V., Moghaddam, S. M., Gao, D., Abernathy, B., Barry, K., Blair, M., Brick, M. A., Chovatia, M., … Jackson, S. A. (2014). A reference genome for common bean and genome-wide analysis of dual domestications. *Nature Publishing Group*, *46*(7), 707–716. https://doi.org/10.1038/ng.3008

Sedlar, A., Zupin, M., Maras, M., Razinger, J., Šuštar-Vozlič, J., Pipan, B., & Meglič, V. (2020). QTL mapping for drought-responsive agronomic traits associated with physiology, phenology, and yield in an Andean intra-gene pool common. *Agronomy*, *10*, 225. https://doi.org/10.3390/agronomy10020225

Sennhenn, A., Njarui, D. M. G., Maass, B. L., & Whitbread, A. M. (2017). Exploring niches for short-season grain legumes in semi-arid Eastern Kenya—Coping with the impacts of climate variability. *Frontiers in Plant Science*, *8*(699), 1–17. https://doi.org/10.3389/fpls.2017.00699

Shavrukov, Y., Kurishbayev, A., Jatayev, S., Shvidchenko, V., Zotova, L., Koekemoer, F., … Langridge, P. (2017). Early flowering as a drought escape mechanism in plants: How can it aid wheat production? *Frontiers in Plant Science*, *8*, 1950. https://doi.org/10.3389/fpls.2017.01950

Shiferaw, B., Tesfaye, K., Kassie, M., Abate, T., Prasanna, B. M., & Menkir, A. (2014). Managing vulnerability to drought and enhancing livelihood resilience in sub-Saharan Africa: Technological, institutional and policy options. *Weather and Climate Extremes*, *3*, 67–79. https://doi.org/10.1016/j.wace.2014.04.004

Singh, V. K., Saxena, R. K., & Varshney, R. K. (2017). Sequencing pigeonpea genome. In R. K. Varshney, R. K. Saxena, & S. A. Jackson (Eds.), *The pigeonpea genome*. Compendium of Plant Genomes. Springer. https://doi.org/10.1007/978-3-319-63797-6_9

Sivasakthi, K., Thudi, M., Tharanya, M., Kale, S. M., Kholová, J., Halime, M. H., … Vadez, V. (2018). Plant vigour QTLs co-map with an earlier reported QTL hotspot for drought tolerance while water saving QTLs map in other regions of the chickpea genome. *BMC Plant Biology*, *18*, 29. https://doi.org/10.1186/s12870-018-1245-1

Sperdouli, I., & Moustakas, M. (2012). Spatio-temporal heterogeneity in *Arabidopsis thaliana* leaves under drought stress. *Plant Biology*, *14*(1), 118–128. https://doi.org/10.1111/j.1438-8677.2011.00473.x

Sreenivasa, V., Lal, S. K., Babu, P. K., Swamy, H. M., Yadav, R. R., Talukdar, A., & Rathod, D. R. (2020). Inheritance and mapping of drought tolerance in soybean at seedling stage using bulked segregant analysis. *Plant Genetic Resources: Characterization and Utilization*, *18*, 1–8. https://doi.org/10.1017/S1479262120000052

Sserumaga, J. P., Kayondo, S. I., Kigozi, A., Kiggundu, M., Namazzi, C., Walusimbi, K., … Mugerwa, S. (2021). Genome-wide diversity and structure variation among lablab [*Lablab purpureus* (L.) Sweet] accessions and their implication in a Forage breeding program. *Genetic Resources and Crop Evolution*. https://doi.org/10.1007/s10722-021-01171-y

Suzuki, N., Koussevitzky, S., Mittler, R., & Miller, G. (2012). ROS and redox signalling in the response of plants to abiotic stress. *Plant, Cell and Environment*, *35*(2), 259–270. https://doi.org/10.1111/j.1365-3040.2011.02336.x

Thilagavathy, A., & Devaraj, V. R. (2016). Evaluation of appropriate reference gene for normalization of microRNA expression by realtime PCR in Lablab purpureus under abiotic stress conditions. *Biologia*, *71*(6), 660–668. https://doi.org/10.1515/biolog-2016-0091

Tian, Y., Zeng, Y., Zhang, J., Yang, C. G., Yan, L., Wang, X. J., … Sheng, J. (2015). High quality reference genome of drumstick tree (*Moringa oleifera* Lam.), a potential perennial crop. *Science China. Life Sciences*, *58*(7), 627–638. https://doi.org/10.1007/s11427-015-4872-x

United Nations. (2019). World population prospects. Department of Economic and Social Affairs, Population Division-United Nations, New York.

USDA. (2012). Lablab (*Lablab purpureus*) plant guide. Retrieved September 9, 2019, from United States Department of Agriculture-Natural Resources Conservation Services website: http://plants.usda.gov/plantguide/pdf/pg_lapu6.pdf

Vaijayanthi, P. V., Ramesh, S., Gowda, M. B., Rao, A. M., & Keerthi, C. M. (2018). Genome-wide marker-trait association analysis in a core set of Dolichos bean germplasm. *Plant Genetic Resources*, *17*, 1–11. https://doi.org/10.1017/S1479262118000163

Valliyodan, B., Lee, S. H., & Nguyen, H. T. (2017). Sequencing, assembly, and annotation of the soybean genome. In H. Nguyen & M. Bhattacharyya (Eds.), *The soybean genome*. Compendium of Plant Genomes. Springer. https://doi.org/10.1007/978-3-319-64198-0_5

Venkatesha, S. C., Ganapathy, K. N., Byre Gowda, M., Ramanjini Gowda, P. H., Mahadevu, P., Girish, G., & Ajay, B. C. (2013). Variability and genetic structure among lablab bean collections of India and their relationship with exotic accessions. *Vegetos*, *26*(Special), 121–130. https://doi.org/10.5958/j.2229-4473.26.2s.130

Vidigal, V., Duarte, B., Cavaco, A., Caçador, I., Figueiredo, A., Mato, A., … Monteiro, F. (2018). Preliminary diversity assessment of an undervalued tropical bean (*Lablab purpureus* (L.) Sweet) through fatty acid profiling. *Plant Physiology and Biochemistry*, *134*, 508–514. https://doi.org/10.1016/j.plaphy.2018.10.001

Villordo-Pineda, E., González-Chavira, M. M., Giraldo-Carbajo, P., Acosta-Gallegos, J. A., & Caballero-Pérez, J. (2015). Identification of novel drought-tolerant-associated SNPs in common bean (*Phaseolus vulgaris*). *Frontiers in Plant Science*, *6*, 546. https://doi.org/10.3389/fpls.2015.00546

Wang, B., Zhao, M., Yao, L., Joao, M. S., Babu, V., Wu, T., & Nguyen, H. T. (2018). Identification of drought-inducible regulatory factors in *Lablab purpureus* by a comparative genomic approach. *Crop & Pasture Science*, *69*, 632–641. https://doi.org/10.1071/CP17236

Wang, Y. H., Qu, X. J., Chen, S. Y., Li, D. Z., & Yi, T. S. (2017). Plastomes of Mimosoideae: Structural and size variation, sequence divergence, and phylogenetic implication. *Tree Genetics & Genomes*, *13*, 41. https://doi.org/10.1007/s11295-017-1124-1

Xu, P., Moshelion, M., Wu, X., Halperin, O., Wang, B., Luo, J., … Li, G. (2015). Natural variation and gene regulatory basis for the responses of asparagus beans to soil drought. *Frontiers in Plant Science*, *6*, 891.

Yadav, S., & Sharma, K. D. (2016). Molecular and morphophysiological analysis of drought stress in plants. In E. C. Rigobelo (Ed.), *Plant growth* (pp. 149–173). InTechOpen. https://doi.org/10.5772/65246

Yang, K., Tian, Z., Chen, C., Luo, L., Zhao, B., Wang, Z., Yu, L., Li, Y., Sun, Y., Li, W., Chen, Y., Li, Y., Zhang, Y., Ai, D., Zhao, J., Shang, C., Ma, Y., Wu, B., Wang, M., … Wan, P. (2015). Genome sequencing of adzuki bean (*Vigna angularis*) provides insight into high starch and low fat accumulation and domestication. *Proceedings of the National Academy of Sciences*, *112*, 13213–13218. https://doi.org/10.1073/pnas.1420949112

Yao, L. M., Wang, B., Cheng, L. J., & Wu, T. L. (2013). Identification of key drought stress-related genes in the hyacinth bean. *PLoS ONE*, *8*(3), e58108. https://doi.org/10.1371/journal.pone.0058108

Young, N. D., & Zhou, P. (2020). The sequenced genomes of *Medicago truncatula*. In F. J. de Bruijn (Ed.), *The model legume Medicago truncatula* (1st ed.) (pp. 828–834). John Wiley & Sons, Inc.. https://doi.org/10.1002/9781119409144.ch103

Yssel, A. E. J., Kao, S., Peer, Y. V., & Sterck, L. (2019). ORCAE-AOCC: A centralized portal for the annotation of African orphan crop genomes. *Genes*, *10*, 950. https://doi.org/10.3390/genes10120950

Zandalinas, S. I., Mittler, R., Balfagón, D., Arbona, V., & Gómez-Cadenas, A. (2018). Plant adaptations to the combination of drought and high temperatures. *Physiologia Plantarum*, *162*(1), 2–12. https://doi.org/10.1111/ppl.12540

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